

Larval biology, life cycle and habitat requirements of *Macromia splendens*, revisited (Odonata: Macromiidae)

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ABSTRACT

Information on larval biology of *Macromia splendens* was compiled and supplemented by hitherto unpublished data. Larvae inhabit mainly calm river stretches, sometimes artificial impoundments, and lentic margins of lotic sections. From the majority of records it is concluded that the larvae mainly dwell in sandy substrates in shallow water, which sometimes contains little leaf litter. Larvae occur in smaller numbers on substrates dominated by coarse detritus or on bedrock in deeper water. Larvae of *M. splendens* are able to burrow in sand, but such burrowing takes a long time, and sometimes parts of their body remain uncovered. Therefore, they are considered shallow burrowers. Based on head-width frequency distributions recorded at the Gardon de Miallet, southern France, the species is believed to require two years per generation.

INTRODUCTION

The southwest European endemic *Macromia splendens* (Pictet) is one of the rarest dragonfly species in Europe (Van Tol & Verdonk 1988; d'Aguilar & Dommangé 1998). It belongs to the six European odonate species that are hitherto listed as threatened by IUCN (2004). Furthermore, *M. splendens* is listed as endangered by the Fauna-Flora-Habitat directive of the European Union (92/43/EEG of 21 May 1992). The FFH directive is regarded as a relatively powerful instrument to protect populations and habitats (Sahlén et al. 2004). Whereas reliable data on the distribution of *M. splendens* in parts of its range are available (Grand & Dommangé 1996; Cordero Rivera 2000; Grand 2002; Malkmus 2002), less is known about habitat requirements and the biology of the species. Van Helsdingen et al. (1996) pointed out that further knowledge of these requirements is necessary to develop conservation measures, such as the designation and management of special areas of conservation. At least some data on adult behaviour are available (Grand & Dommangé 1996; Schütte & Suhling 1997), including a mark-release-recapture study that was carried out by Cordero Rivera et al. (1999). Information on habitats is usually based on observations of adults or records of exuviae (e.g. Lieftinck 1965; Bilek 1969; Tiberghien 1985; Malkmus 1996b, 2002, 2003).

No further information on larval ecology has been published since Grassé's (1930) observation of larvae half-buried in mud in lentic parts of running waters. Several authors indicate that they have caught or observed larvae (e.g. Grand & Dommanget 1996; P. Jahn in Jödicke 1996; Chelmick 2004). However, little or no information on larval biology was provided in these studies. Later, Leipelt et al. (1999) presented results of habitat selection experiments, which confirmed the findings of Grassé on the whole, but, at that time, the exact microhabitat containing most of the larval population was not known with certainty. More recently, new data on larval microhabitat and duration of larval development were provided (Leipelt et al. 2001), which has stimulated collection of further data since that time.

The aim of this paper is to make these data on larval ecology of *M. splendens* more widely available, to report our own data, and to discuss the overall findings in the context of contradictory statements about the distribution of larvae.

STUDY SITES AND METHODS

Information on the species' habitat and larval biology was compiled from the literature and broadened by new field data.

During our own studies, running water sites along the Gardon river system (Département Gard, southern France) were surveyed and especially searched for exuviae. The major study site was situated in the middle course of the Gardon de Mialet, 160 m a.s.l., 10 km upstream of Anduze (44°07'N, 3°55'E). The bottom of the valley was 50-100 m broad, the river course being at most 23 m in width. The slopes on both sides of the river reached up to ca 500 m and were densely overgrown by forest dominated by oak and chestnut trees. Alder, willow and poplar trees lined the banks, which, at intervals, consisted of rocky cliffs up to several metres high. The river course varied between shallow riffles between gravel banks with high current up to 1 m s⁻¹ and more during floods and deep pool sections where the current was hardly measurable at certain seasons. Along a river stretch of ca 1.5 km – our main study site – we searched intensely for larvae and took records of the corresponding meso- and microhabitats. Larvae were caught by using a hand net with a pentagonal opening (width at the bottom side: 30 cm, mesh size: 0.5 mm) and a 1-m-long handle, employing the kick-sample method. The sampling was non-invasive, i.e. no larvae died during sampling, and after the procedure all individuals were released at the sample sites. The size of the larval population in the studied stretch remained at a very stable level over the years. We recorded the type of substratum at the sample sites and the water depth. The current velocity was roughly estimated by the float method.

Sampling was conducted on the following dates: 13-17 July 1999, 15-18 June 2000, 23-24 May 2002, 26-29 July 2003, and 7-11 August 2004. Life-cycle duration was estimated by analysing the larval-size frequency distribution as recorded in the field. We measured the larval head widths using a dial calliper (accuracy: 0.01 mm). Assuming that, on average, a 1.25-1.3-fold increase in head width takes place from one larval stadium to the next larger one (cf. overview in Corbet 1999: 210), the stadia were classified based on the head widths of the exuviae collected at the Gardon de Mialet. Although we did not have subsequent monthly data recorded within one single year, we listed our data in month order, independently of the year of study. We are aware that this method does not allow us to track the develop-

ment of the individuals in a single generation and was therefore not very precise. However, together with phenology and emergence data derived from own observations and from literature the method still allows a good estimate of voltinism of this rare species.

DISTRIBUTIONAL RANGE

Macromia splendens is endemic to southwestern Europe, i.e. southern France, Spain and Portugal. Since comprehensive data on the distribution of *M. splendens* are available for France (Grand & Dommange 1996; Grand 2002), Spain (Cordero Rivera 2000), and Portugal (Malkmus 2002), we will provide only brief information on latitudinal and longitudinal distribution and climate.

According to Grand & Dommange (1996), *M. splendens* requires very warm localities in southern France and is usually restricted to altitudes up to 350 m, although exceptions occur. M. Lohr (pers. comm.) found exuviae in the Tarn valley at an altitude of ca 480 m. In Galicia, north-western Spain, the species inhabits low-altitude rivers up to 250-300 m (Cordero Rivera 2000). The record for the highest altitude at which larvae have been found comes from a site at 640 m (cf. Cordero Rivera 2000). In north eastern Portugal, patrolling males were observed at 680 m (Malkmus 2002).

Although *M. splendens* is considered to be a running-water species, longitudinal distribution patterns have not previously been taken into account. Here, we will present preliminary data from our distribution study at the Gardon de Miallet. The river section hosting the relatively large larval population was ca 36 km downstream from the uppermost source. Few records originated from upstream sections of the river: one exuvia and two larvae were found at 21 km and one exuvia at 30 km downstream from the uppermost source. Larval records at the Cèze River and at the Chassezac River were obtained at sites located 37 and 62 km, respectively, downstream from the source (own unpubl. data). Heidemann & Seidenbusch (1993) indicated that *M. splendens* was even found in the vicinity of a spring-source pool. However, it is not clear whether that pool was the uppermost source. The most downstream-situated records originate from the Lot River, near Cahors, ca 225 km away from the source (Lieftinck 1965). At the Hérault River, adults were observed 37 km downstream from the uppermost source; exuviae were abundant in the river between 50 and 70 km from the source and were even recorded a few kilometres from its mouth into the sea, which is 160 km from the source (M. Lohr pers. comm.).

From the distribution of records in Galicia, Cordero Rivera (2000) concluded that the species inhabits areas with mean annual temperature over 13°C and is limited to regions with clement winters. This assumption seems to be transferable to southern France, where at least all localities with records after 1950, as mapped by Grand & Dommange (1996), are also within this 13°C isotherm (cf. Pagny 1988). Some evenly-warm regions in the Provence east of the Rhône River appear, however, not to be colonized, although some apparently suitable river courses are present. Grand (2002) stressed that the colonization of these habitats may be inhibited by the strong northern winds in the Rhône River valley (Mistral), which commonly blow during the flight season of *M. splendens*. Also, low dispersal ability was inferred (Grand 2002).

MESOHABITAT

Several descriptions of watercourses inhabited by *Macromia splendens* are available (e.g. Lieftinck 1965; Grand & Dommangé 1996; Malkmus 2002, 2003). According to these authors, the larvae occur mainly in calm parts of rivers, sometimes in natural or artificial impoundments (Grand & Dommangé 1996; Cordero Rivera 2000). Some authors stress the extensive depth and the lake-like appearance of such stretches (Bilek 1969; Grand & Dommangé 1996). Cordero Rivera (2000) found exuviae even at a deep, elongated reservoir. Others point out that inhabited watercourses can be characterized by high variance of depth and structural richness associated with deep pools, rocks protruding from the water, and sand and gravel banks (Leipelt et al. 1999; Malkmus 2003). River margins are often formed by walls of rock or dominated by dense shrubbery (Heidemann & Seidenbusch 1993; Grand & Dommangé 1996). The species dwells in broad streams and large rivers up to 100 m or more in width (Lieftinck 1965; Grand & Dommangé 1996). In Portugal, however, patrolling adult males and even exuviae have been recorded at small brooks, only 2-3 m wide (Malkmus 1996; M. Lohr pers. comm.). In southern Portugal, adults occur even at rivers that often dry out during summer and leave only chains of pools in the riverbed (Malkmus 2003). But it is not known with certainty whether the species undergoes development in such river sections.

Physico-chemical parameters of the species' habitat are indicated by several authors. Cordero Rivera (2000) provides information on these parameters in inhabited watercourses in Galicia. He detected no significant differences between rivers with *M. splendens* populations and those rivers without. Average water temperature for seven rivers inhabited by this species is given as $17.7^{\circ}\text{C} \pm 0.5$ (Cordero Rivera 2000). The measured temperatures at two sites that contained this species in a tributary of the Guadalquivir in southern Spain are 24 and 25°C (Ferreras Romero 1988). Unfortunately, in both cases the time and date of data acquisition were not mentioned. In southern France, the values in mid summer ranged between 22 and 26°C (Grand & Dommangé 1996; Grand 2002). Such values are also typical of the Gardon de Miallet: in mid June 2000 and in mid July 1999 the water temperature reached 22.1 and 24.0°C , respectively (Leipelt & Suhling 2001). Further data are indicated for Galicia (Cordero Rivera 2000), Andalusia (Ferreras Romero 1988), and the Gardon de Miallet (own unpubl. data): pH-values in order of citation: 7.26 ± 0.152 , 8.3/8.4, and 7.5; conductivity values: $70.1 \pm 17.48 \mu\text{S cm}^{-1}$, not indicated, and $90 \mu\text{S cm}^{-1}$; oxygen concentration: $8.99 \pm 0.117 \text{ mg l}^{-1}$, 8.0/9.9 mg l^{-1} , and not measured.

LARVAL MICROHABITAT

Information on larval microhabitat of *Macromia splendens* has been scarce for a long time. Grassé (1930) was the first to describe larval distribution in this species. He found the larvae half-buried in mud in calm parts of running waters. Lieftinck (1965) found that exuviae were only thinly coated with mud particles and concluded that older stadia of *M. splendens* are superficial burrowers or live among benthic material with a distinctly soft, muddy character. D'Aguilar & Dommangé (1998) indicated that larvae dwell in muddy or sandy substrates. The larvae are

thought to hunt by ambush and to occur in both shallow and much deeper river sections (Heidemann & Seidenbusch 1993). According to Grand & Dommangé (1996) calm and rather warm stretches of running waters are the typical larval habitats; these are characterized by extensive width and a depth up to 5-6 m. In faster flowing rivers, larvae may be restricted to pools; populations in such rivers are thought to be smaller compared with those occurring in larger water bodies (Grand & Dommangé 1996). However, since the work of Grassé (1930), no further details on larval observations were provided until 1999.

Leipelt et al. (1999) conducted substrate-choice experiments under field conditions using four larvae of the penultimate stadium. They found that the larvae prefer leaf detritus on sand rather than bare sand or stones on sand. Furthermore, shaded substrates are selected rather than substrates exposed to the sun. During the day the larvae are inactive, lying under leaves or buried in the sand; they become active only at night. After release in the calm river stretch, where they had been caught, the larvae were observed to swim immediately towards the bottom. Propulsion is performed in the usual anisopteran way, by ejections of water from the respiratory chamber. The larvae swim with forelegs and hindlegs outstretched forward and backward, respectively. When they arrived at the sandy bottom in shallow water, they paused for 15-25 s. Then they began to grope with their hindlegs. After additional intervals of 15-390 s, the larvae began to burrow with vigorous lateral swaying of their abdomen at a rate of two or three times per minute. When ca one third of the abdomen was covered with sand, the abdominal movements ceased and the larvae began to use their legs to sweep sand over their bodies. At 5 to 18.5 min after burrowing began, only the head and legs remained uncovered (Leipelt et al. 1999).

Feeding behaviour has been observed by Butler (1985), who apparently regards larval *M. splendens* as bottom dwellers: in captivity the larvae detected prey up to distances of 5 mm. Sometimes the larvae even leapt up in order to intercept worms that had been dropped into the water, but were occasionally alarmed by tadpoles. In contrast to all the former observations, Cordero Rivera (2000) suggests that larvae of *M. splendens* inhabit tree roots. His conclusion is based on observations of one larva that was close to emergence and was resting on a tree root. Additionally, Cordero Rivera et al. (1999) found three more larvae at a depth of 0.3-1 m at a place where the river bank was dominated by tree roots, dead leaves and branches. Cordero Rivera (2000) emphasizes that none of the larvae was found at the bottom of the river. However, data basing on samples taken at the Gardon de Mialet during three years (Leipelt et al. 2001) give a different view. The following three microhabitat types were found to be occupied (Fig. 1): (I) 53 larvae were found at sandy patches with little leaf litter in shallow water (depth: < 0.35 m) near the river margin; in the majority of cases the sandy layers were only a few millimetres thick, covering rock ledges. (II) Five individuals were recorded in deposits of a mixture of twig, leaf and fine detritus in deep water (0.8-1.2 m), and (III) nine individuals on bedrock in deep water as well (0.8-1.2 m). All larvae occurred in reaches where the water current was hardly noticeable. In later years, 2002-2004 (own unpubl. data), 124 additional larvae were found on the same types of microhabitats and in a similar ratio. In spite of intensive sampling in microhabitats such as alder roots (cf. Leipelt & Suhling 2001) and head-sized boulders, no larvae of *M. splendens* could be found among these substrates. In exceptional cases, individuals were caught on

coarse gravel sparsely covered with twigs and leaf litter. In late July 2003, all 28 small larvae that had apparently hatched in that year were found in the same microhabitats inhabited by the larger larvae. However, compared with the latter, the young larvae tended to occur more frequently on rock ledges that lacked a well-developed sand layer. Nevertheless, it should be mentioned that the ledges were not completely bare but were partly covered with soft fluffs of fine detritus and algae. Two small larvae were introduced into a water-filled bowl with sand at the bottom; they buried themselves in the same manner as described above for larger individuals. According to our findings at the Gardon de Mialet over several years, we believe that larvae of *M. splendens* inhabit calm river sections and lentic margins of lotic river sections.

A cross-section of the typical habitat where most of the larvae were recorded is shown in Figure 1. Walls of steep rock shaped the right river margin, whereas the left margin was characterized by an extensive gravel bank.

During the summer, there was little or no water current over the whole cross-section. A few hundred metres downstream, larvae occupied another stretch that was lotic in the middle of the river bed and showed a calm reach at one margin. A steep bank, which was partly rocky and partly loamy and roofed by trees, shaped this margin. Some rocks protruded from the water and there were sand and detritus deposits at the bottom; these deposits were inhabited by the larvae. The middle of the river bed was covered with gravel and stones, the other margin was shaped by an extensive gravel bank.

LIFE CYCLE

Data on the phenology of *Macromia splendens* are available for southern France and for north-western Spain and Portugal. The earliest observations of adults originate from SE Portugal; the records there in mid April of 1995 and 1997 may be a consequence of unusually warm weather conditions during spring (Malkmus 1996a, 1998). In NE Portugal, adults patrolled in late May or in early June (Malkmus 1996b, 2002). In Galicia (NW Spain) at places continuously monitored, the first exuviae of the year were recorded in mid May 1997 but not before mid June in 1995 and 1998; in the same area, full-coloured adults were on the wing from 22 June to 17 July 1998 (Cordero Rivera et al. 1999). For southern France, Grand & Dommange (1996) found that emergence takes place in the last week of May; just before the middle of June the first specimens reappear at the rivers. However, in some years emergence may occur later. In the first week of June 2004 emergence had apparently not yet taken place at the well-studied section of the Gardon de Mialet (I. Schrimpf and C. Schütte pers. comm.). On 10 June 2004 two exuviae were eventually found there (H. Wildermuth pers. comm.).

In southern France, oviposition takes place in June/July, but only rarely in August (Grand & Dommange 1996; Schütte & Suhling 1997). The flight season may last until mid August (Chaussadas & Dommange 1988) but the best period to observe adults is between mid June and mid July (Grand & Dommange 1996). According to Grand & Dommange (1996) embryogenesis lasts ca 20 days. From this information we conclude that these authors reared the eggs, although this is not stated.

Few assumptions on duration of larval development of *M. splendens* have been made. Lief tinck (1965) suggests a biennial or triennial larval development process. According to observations by Dommange (Grand & Dommange 1996), larval development lasts 22-23 months, starting in July/August and ending in May/June two years later. However, the method of recording these data is not described. In Galicia, in addition to two larvae close to emergence, Cordero Rivera et al. (1999) collected two small larvae, both 5.8 mm in length, in late May 1997. Reared in the laboratory at ca 20°C and fed ad libitum, the larvae reached the final stadium in November 1997. Hence Cordero Rivera et al. (1999) infer that, in the field, larvae need three years to finish their development. It is possible that the authors considered laboratory temperatures to be significantly higher than those in Galician rivers and impoundments.

Head-width frequency distributions, recorded at one and the same river section of the Gardon de Mialet, southern France, during five different seasonal sections over six years (1999-2004; Leipelt et al. 2001, and unpubl. data), indicate a biennial development, at least for the investigated headwater of the Gardon River (Fig. 2). In late May 2002, two larval cohorts existed. Larvae with head widths exceeding 7 mm belonged to the ultimate stadium (F-0); they were close to emergence. All the other larvae were spread over five stadia (F-6 to F-2) and probably belonged to the succeeding cohort. In mid June 2000 no F-0 larva was recorded. At that time, only one larval cohort existed. In mid July 1999 the situation was similar, but most larvae were in the F-2 stadium. In late July 2003 very small larvae were found. Apparently they had hatched from eggs that were laid in that year. The antecedent cohort was spread over only two stadia (F-1 and F-2). In early August 2004, one larva of the ultimate stadium was detected but most larvae were in the penultimate stadium (F-1). Only one small larva was caught, which had hatched during the same summer. Here it should be taken into account that the warm weather typical of summer began early in 2003 but late in 2004.

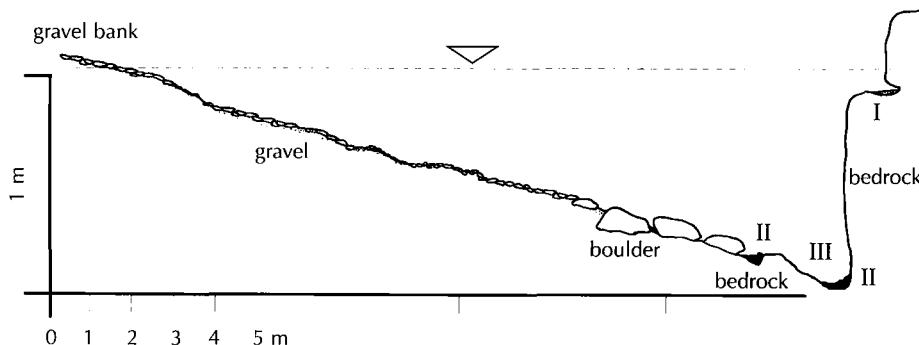


Figure 1: Schematized cross-section of the riverbed of the Gardon de Mialet at a stretch with high numbers of larval *Macromia splendens*. Roman digits indicate the larval microhabitats: I: sand with few leaf litter in shallow water (< 0.35 m); II: mixture of fine and coarse detritus in deep water (0.8-1.2 m); III: bedrock in deep water (0.8-1.2 m). Other substrate types like gravel, boulder and alder roots contained no larvae. Alder roots were absent at this cross-section.

In general, the head-width frequency distributions need to be assessed with caution, since they derived from different years. However, phenological differences occurring between years appeared not to interfere with the general view. From the recorded frequency distributions we conclude that larval development takes 22-23 months. Thus the assumption of Grand & Dommanget (1996) is confirmed. We have no clear evidence of cohort splitting, although in late May 2002 the succeeding cohort was spread over five stadia. In late July 2003 and early August 2004, the corresponding cohorts consisted of only two stadia. There is no doubt that all larvae of such a cohort usually reach the final stadium between late July and September in the studied river section. Therefore, individuals that emerge in May/June of the next year spend the winter in the ultimate stadium. This assumption is confirmed by the absence of the penultimate stadium in late May 2002. Based on all findings at the Gardon de Mialet, *M. splendens* is considered a spring species sensu Corbet (1962).

CONCLUSIONS

According to our results *Macromia splendens* requires two years per generation, at least at the Gardon de Mialet. It has to be verified whether this finding is also valid for other regions, especially those with cooler summers. Little information on size frequency distributions of other *Macromia* species that occur in the subtropics is available. Fukui (1982) assumes that *M. daimoji* Okumura and *M. amphigena* Selys need two years and two to three years per generation, respectively, in the Japanese prefecture of Shizuoka (ca 35°N). According to Smock (1988) the entire development of *M. illinoiensis georgina* (Selys) lasts about two years in South Carolina (ca 33°N). Hence, *M. splendens* seems to follow the life cycle character of its con-generics occurring in the subtropics.

Habitat selection and morphology of East-Asian *Macromia* species have been studied by Lieftinck (1950). He divides the species into two main ecological-morphological groups, consisting of species that live in vegetation or root mats and species that inhabit sandy substrates. Species such as *M. erato* Lieftinck and *M. gerstaeckeri* Krüger that belong to the last group, the so-called sand-dwellers, are characterized by the following traits: a pale sandy yellow colouration showing a fine mottled pattern of light brown; a broad and very flattened abdomen; exceptionally long and spidery legs; and, the ability to burrow in sand. Corbet (1962) regards them as having become shallow burrowers secondarily. Their method of burying themselves differs from that shown by Gomphidae, Cordulegastridae and Libellulidae, probably because sand-dwellers of the genus *Macromia* have long legs ill-adapted for digging (Corbet 1962). Since the above-mentioned traits are also typical of larval *M. splendens* – the abdomen of the exuvia lacks the flatness and colouration of the larva – we propose that this species also belongs to the sand-dweller group (cf. Leipelt et al. 2001). However, it is not clear whether or not *M. splendens* is a near relative of the other members of this group or if the sand-dweller group is heterophyletic.

Due to the ability to burrow in sand *M. splendens* larvae have the opportunity to exhibit a highly cryptic feeding posture similar to that of the Cordulegastridae (cf. Heymer 1973). This may facilitate foraging and avoiding predation. We doubt that remaining buried plays a major role in preventing sand-dwellers from being dislodged and carried away by water currents, as suggested by Lieftinck (1950).

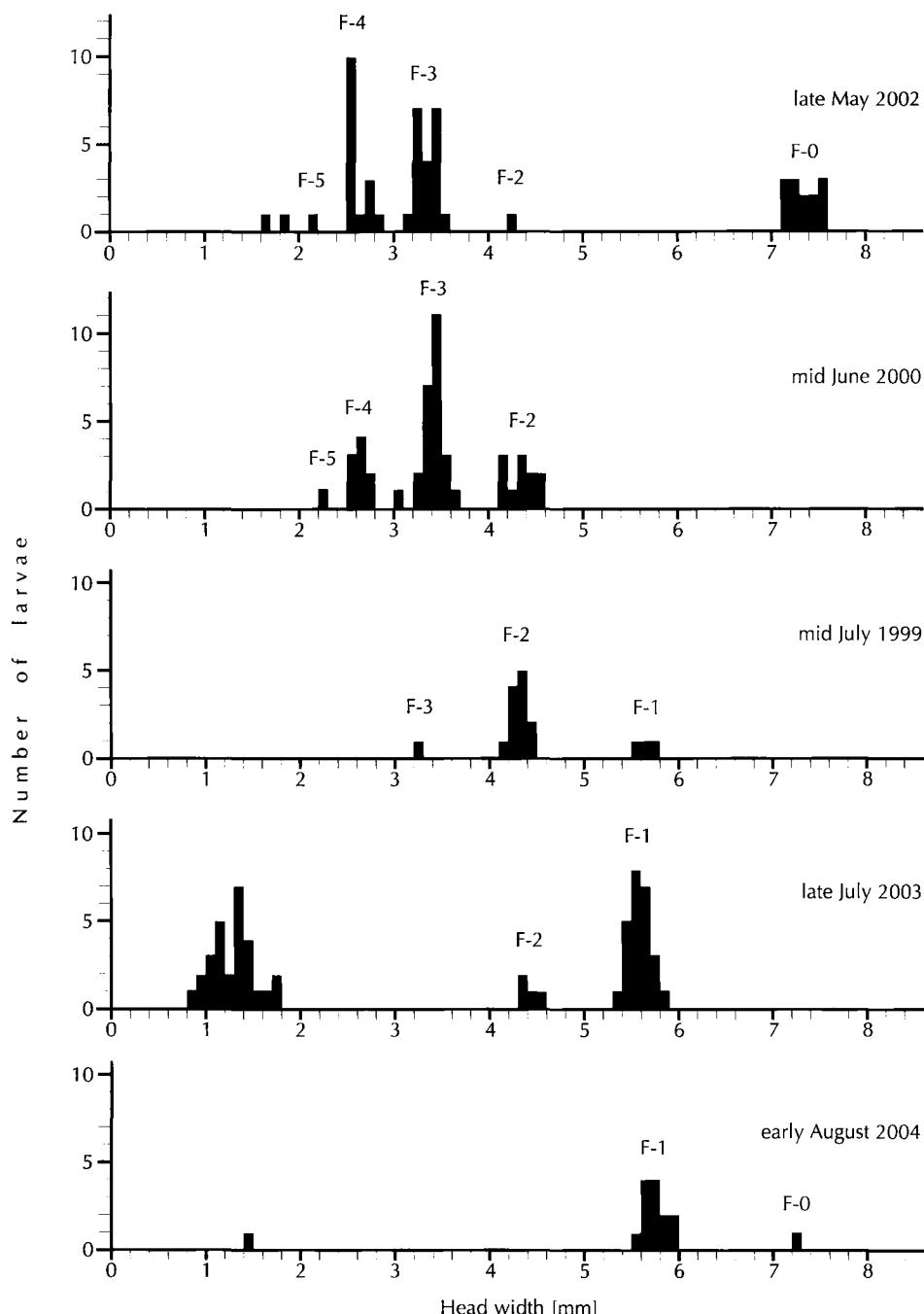


Figure 2: Head width frequency distribution histogram of larval *Macromia splendens* recorded at a river stretch of the Gardon de Mialet investigated at five different times over the course of six years (1999-2004).

Sand is easily carried downstream by water current, and a stronger current would either uncover shallowly buried larvae or cause coverage of larvae by sand. In the latter case, sand dwellers with their long, spidery legs would probably be incapable of freeing themselves from thick sand layers. Perhaps this is one of the reasons why *M. splendens* prefers lentic microhabitats. In our opinion suitable meso- and microhabitats are characterised by permitting sedimentation of fine-grained substrates and/or detritus; high sedimentation rates should not occur though. However, there is insufficient information on what happens during spates. It remains unclear how populations can withstand heavy spates peculiar to rivers such as the Ardèche (cf. Mérigoux & Dolédec 2004). On 8 and 9 September 2002, in the catchment of the Gardon, massive rainfalls occurred and caused heavy inundations (Direction Régionale de l'Environnement Languedoc-Roussillon 2002). However, according to our sampling results it seems that the flood did not affect the population of *M. splendens* at the surveyed site of the Gardon de Mialet.

Information on distribution of *M. splendens* suggests rather continuous distribution areas in southern France and Portugal (cf. Grand & Dommangé 1996; Malkmus 2002). Large gaps occur in Spain (cf. Cordero Rivera 2000). Further investigations are needed to determine whether these gaps are the result of insufficient observations or whether they are, in fact, real gaps in the distribution of the species. It is still unclear which factors are responsible for the species' restriction to the southwest of Europe, although the average annual 13°C isotherm may be an explanation. *M. splendens* is thought to require a warm or mild climate (Grand & Dommangé 1996; Cordero Rivera 2000). However, nothing is known about the species' 'vagility' a poor ability to disperse (cf. Grand 2002) could contribute to such a limitation of range. Knowledge about microhabitat and mesohabitat requirements has increased over the last years, but macrohabitat requirements are still unclear. Surveys on catchment characteristics such as geology, discharge, gradient, sediment load, natural and artificial impoundments, and forest structure are necessary to determine the importance of these factors (cf. Cordero Rivera 2000; Malkmus 2003). Exact data on longitudinal distribution patterns within catchments and further information on larval and adult behaviour would be desirable as well. Additionally, more reliable data on population size, fluctuations at the inhabited catchments, and on exchange between populations are required to assess the status of endangerment more properly.

Thus, great advances in knowledge about distribution, ecology and behaviour of *M. splendens* have taken place in the last 20 years. However more knowledge of this species is required in order to better protect it.

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